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RESOURCE ACQUISITION IN THE PRESENCE OF A NOVEL STIMULUS  
BY COYOTES OF DIFFERENT SOCIAL RANK

by

Warren E. Johnson

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Fisheries and Wildlife Ecology

Approved:

Major Professor \_\_\_\_\_

Committee Member \_\_\_\_\_

\_\_\_\_\_  
Dean of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

1984

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ABSTRACT

Resource Acquisition in the Presence of a Novel Stimulus

by Coyotes of Different Social Rank

by

Warren E. Johnson, Master of Science

Utah State University, 1984

Major Professor: Dr. David F. Balph  
Department: Fisheries and Wildlife

This study investigated the acquisition of food by hand-reared coyotes, Canis latrans, of different social rank in a familiar area with and without novel objects (safe and potentially unsafe conditions). The first objective was to test the hypothesis that dominant animals are more hesitant than subordinates in approaching food in the presence of a novel stimulus. The results were that dominant pups usually were the first to feed in the absence of novel stimulus, and subordinate pups were the first to feed when novel objects were present. The second objective was to see if the behavior of subordinates in the above test was caused by the presence of a

## INTRODUCTION

Dominant-subordinate relationships strongly influence individual behavior. The dominant animals in a group generally control access to resources such as food (e.g. Wrangham 1981) and mates (e.g. McClintock et. al. 1982). To survive, the more subordinate animals are forced to obtain resources not controlled by the dominant animals. One way they accomplish this is to acquire resources at the periphery of the group (see Struhsaker 1967; Fretwell 1969). Such resources may be marginal in quality or quantity and require more effort and ingenuity to obtain than the resources at the center of the group controlled by the dominant animals.

Another way of avoiding higher-ranking animals is for subordinate animals to be less cautious than dominant animals in investigating and exploiting resources in potentially dangerous situations. For example, differences in response to novel objects (presumably potentially dangerous) by individuals of different social ranks have been shown in rats (Rattus norvegicus) (Robertson 1982), chaffinches (Fringill coelebs) and sparrows (Passer domesticus) (Turner 1965), jackdaws (Corvus monedula) (Katzir 1982, 1983) and japanese macaques (Macaca fuscata) (Miyadi 1964; Menzel 1966). Hegner (in press) similarly found that lower-ranking blue-tits (Parus caeruleus) resume



feeding more rapidly than dominants when the danger from predators is high.

There are at least two explanations possible for explaining the less conservative behavior shown by lower-ranking animals in a potentially dangerous situation. First, the phenomenon could be due to the presence of dominant animals. Subordinates may be simply making "the best of a bad situation", obtaining resources by the best available method (Pulliam & Caraco 1984). When alone, or when made possible by extensive resource availability, subordinates might be expected to behave more cautiously, just as a dominant individual.

Alternatively, the response of more subordinate animals in a dangerous situation could be an alternative method of resource acquisition, which after an initial period of learning, is not directly influenced by dominants. In the process of having to work harder to obtain more limited resources in marginal environments, lower ranking animals may have learned to be less conservative. Subordinates could therefore be employing an alternative strategy which they continue to demonstrate even in the absence of higher-ranking animals.

This study sought to investigate the role of social rank on food acquisition in coyotes (Canis latrans) of different social rank in the presence and absence of a novel stimulus. Specifically, the first

objective was to test the hypothesis that, when in a group, dominants are more hesitant than subordinates in approaching food in the presence of novel objects. The coyote is a good species with which to test the generality of the hypothesis because although coyotes readily form dominance hierarchies (Allender & Balph 1972; Bekoff 1978; Knight 1978), they are not a highly social species, and they exhibit great flexibility in social structure (Camenzind 1978; Bekoff & Wells 1981; Bowen 1981).

The second objective was to determine if the behavior of the subordinates was caused by the presence of a higher-ranking animal, or alternatively, was a response (once learned) that occurred independent of the dominant's presence.

## METHODS

The facilities and animals for this study were provided by the Predator Ecology and Behavior Project of the U.S. Fish & Wildlife Service, Utah State University, Logan, Utah. Test animals were removed from their mothers 10-12 days after birth. They were reared by hand to facilitate handling and to allow the formation of equal sized groups. Hand-reared pups also adjust to human observation more quickly than nonhand-reared pups (Knight 1978).

Between 15 and 18 days of age, the pups were combined into groups of four individuals of the same sex and approximate age. Siblings remained together, but often were placed with nonsiblings to create equal sized groups. Between 7-8 weeks of age, a bacterial infection (Campyrobacter jejuni) reduced the original number of pups, necessitating the further combination of several groups. This final combination left three groups with three pups and one with four pups (Table I).

Groups were raised in 0.1 ha teardrop-shaped pens. A den box and an observation room with one-way glass adjoined each pen (Fig. 1).

Social ranks within groups were determined by the outcome of social encounters called "dominations". When the pups were between 5

Table I. Pup History

Group	Pup	Sex	Birthday*	Age Combined
A	1	M	4-19	8 weeks
	2	M	4-19	
	3	F	4-16	
	4	M	4-15	
B	1	M	4-22	2 weeks
	2	M	4-22	
	3	M	4-25	
C	1	F	4-27	2 weeks
	2	F	4-27	
	3	F	4-27	
D	1	M	4-11	7 weeks
	2	M	4-11	
	3	M	4-15	

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\* Pups born on the same date are siblings.

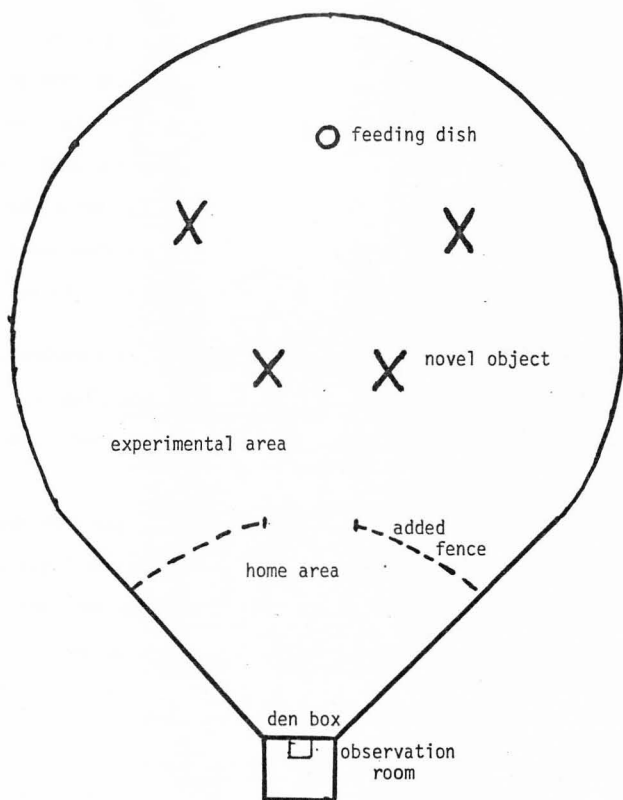


Fig. 1. Diagram of the pen and observation room.

and 8 weeks of age all observed dyadic interactions which included a growl, pin, hip-slam, threat-face or bite and terminated with one pup rolling over to the other were recorded (described by Knight 1978). The pup that rolled over (or the last to roll over) was considered the loser. When one member of the dyad consistently lost to the other it was considered the subordinate. Observations of the interactions of each group were conducted during times of activity several times each 24 h period.

Dominance at food was determined for each dyad over a period of days. A small portion of a rabbit carcass was placed in the pen with two pups. Both pups had already eaten their regular food (ground mink chow) and had previously been exposed to similar rabbit carcasses. The dominant was considered to be the animal that could displace the other pup from the carcass and spend more time feeding on the carcass until the food was completely consumed. This experiment was repeated several times until a pup won three contests in a row, irrespective of which individual got the carcass first.

#### Testing Coyotes in Groups

Between 13 and 14 weeks of age, a fence with a 10 m wide gate was constructed in the experimental pen, dividing the pen into home and experimental areas (Fig. 1). After 5 days of acclimation to the

fence, the pups were enclosed in the home area and testing began. Sessions were conducted between 0600 and 1000 hours, 7 days per week and lasted 25 min. Prior to each session the pups were enclosed in their den box, the gate to the experimental area was opened, and a food dish filled with their regular food, ground mink chow, was placed in the experimental area.

Sessions began by opening the den box from the observation room, which allowed the pups to reenter the pen without disturbance. After each session the pups were enclosed in the home area and fed until satiated to insure all pups would be equally hungry for the next session.

Initially each group was tested for several sessions under familiar conditions to establish a base from which changes could be measured. These data, collected by scan sampling (Altmann 1974) every 30 s, consisted of the location and feeding activity of each animal. The amount of time it took each animal to enter the experimental area and to commence feeding was also recorded. After at least seven sessions under familiar conditions, four 46 X 51 X 76 cm wire-mesh boxes were arranged as shown in Fig. 1. These objects, a novel stimulus for the pups, were handled with gloves to reduce the amount of scent that became associated with them. A visual stimulus was chosen because visual cues are easiest to manipulate and because vision is relatively more important than hearing and smell to the

coyote when searching for food (Wells & Lehner 1978).

Each group was then tested with these novel objects (hereafter termed unfamiliar conditions) for several sessions until the pups showed habituation to the objects by initiating feeding as rapidly as they had when the objects were absent. The process was then repeated with another novel stimulus and another period of habituation. This second time, the novel stimulus consisted of rearranging the wire-mesh boxes around the feeding dish, so the pattern was novel, but not the objects.

#### Testing Coyotes Individually

The individual tests were conducted to determine if patterns shown by each animal when within the group persisted when alone. Testing sessions were conducted daily between 0600 and 0900 hours and lasted 20 min for each animal. The pups were released individually from the den box and allowed to feed from the food dish, which was located in the center of the home area. While not being tested, the other pups of the group were kept in a separate den box in the observation room.

The time it took for pups to commence feeding was recorded for several sessions. Once behavior under these familiar conditions was established, the novel stimulus was introduced. The novel stimulus,



one of the same wire mesh boxes used in the group test was placed 2 m from the feeding dish in the home area. Sessions continued until baseline responses (under familiar conditions) had been reestablished. Pups which did not eat during a session were not fed until after 3 days of sessions, so that they would not learn that they could obtain food without approaching the dish.

### Statistical Analysis

For analysis of the group tests, the dominant pup of each group was compared with all others (subordinates) in that group. For each group session it was determined which pup entered the experimental area first and which fed first. If more than one pup commenced the activity simultaneously, each was considered an "initiator". For each group, the percentage of times a dominant or subordinate was an initiator was determined for the sessions with and without the novel objects. The first two sessions after a novel stimulus had been introduced were used to determine responses to novel stimulus (unfamiliar conditions), and the other sessions were defined as not having a novel stimulus (familiar conditions) (Fig. 2). The mean percentage for all the groups was obtained for both conditions and compared, with the aid of t-tests, with what would be expected if the initiators were simply determined by chance.

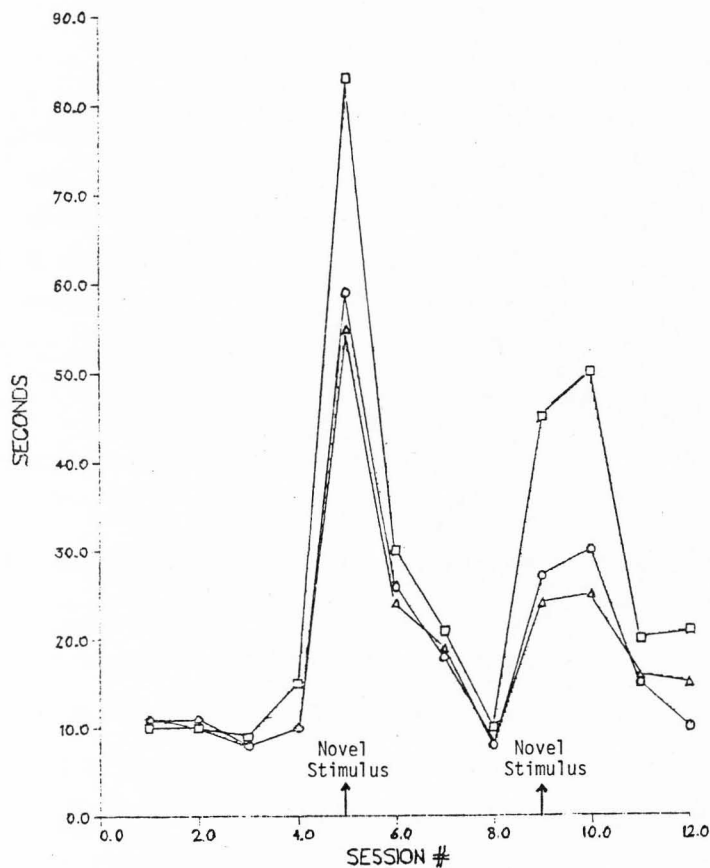


Fig. 2. An example of typical response patterns of the pups with and without a novel stimulus when tested in a group. Results from group B; circles represent pup #1, triangles pup #2 and squares pup #3. Sessions 1, 2, 3, 4 and 8 are without novel stimuli and sessions 5, 6, 9 and 10 represent conditions with a novel stimulus.

The results of the individual tests were compared using analysis of variance. The four sessions following the introduction of the novel stimulus were classified as conditions with a novel stimulus, and the four previous sessions were considered to be without novel stimuli (familiar conditions). The differences in the amount of time it took each pup to commence feeding under conditions with and without a novel stimulus were then compared.

## RESULTS

### Social Ranks

The determination of social rank within each group by the number of dominations and by the determination of dominance at food yielded the same social ranks for each group (Table II). Fewer dominations were recorded in group A because of the relatively late formation of the group.

### Testing Coyotes in Groups

Qualitative Results. The pups showed strikingly different response patterns with and without the presence of the novel stimulus. Without the novel objects, upon release from the den box, the pups ran quickly through the gate toward the food dish where they ate together. Because the food dish was virtually an unlimited food source, dominants pups rarely exerted control over the food, exercising their influence on the others only for rabbit carcasses. With the novel objects present, the pups similarly ran from their den box towards the food. Once they noted a difference in the experimental area, however, they approached the food more slowly. This "caution" was either first displayed in the home area or in the experimental area, depending upon where the pups appeared to first note a change.

Table II. Determination of Social Rank by Number of Dominations and by Dominance at Food.

		Winner			
		No. dominations (No. wins in food dominance tests)			
Group	Pup	1	2	3	4
	1	-	-	-	-
	2	16 (3)	-	(1)	-
	3	6 (3)	4 (4)	-	-
	4	5 (4)	5 (3)	14 (3)	-
Group B	Pup	1	2	3	
	1	-	-	-	
	2	25 (3)	-	-	
	3	37 (3)	43 (3)	-	
Group C	Pup	1	2	3	
	1	-	-	-	
	2	3 (3)	-	-	
	3	36 (3)	12 (4)	-	
Group D	Pup	1	2	3	
	1	-	-	-	
	2	9 (3)	-	-	
	3	18 (3)	21 (3)	-	

Instead of immediately approaching the food dish as before, the pups now showed classic approach-avoidance behavior (Miller 1959). They moved towards the dish, and then often hastily retreated. They also circled the dish and the novel objects. Eventually, one neared the feeding dish and ate some of the food. This initial foray was followed by either a rapid withdrawal, or the approach to the dish by another groupmate.

Usually, by the third session after the introduction of the novel stimuli, the pups appeared habituated to the novel objects and ran directly toward the food dish (Fig. 2). Rearranging the wire-mesh boxes again slowed the pups approach to the food dish, although not by as much as before. Throughout these sessions, the pups avoided the wire-meshed boxes with only two pups approaching within 2 m of the novel objects.

Quantitative Results. Both in the presence and absence of the novel stimulus, there were no significant differences between the frequencies that either dominants or subordinates initiated entrance into the experimental area and what would be expected by chance (Table III). Dominants initiated feeding significantly ( $p < 0.05$ ) more often than would be expected by chance without the novel stimulus. Dominants also initiated feeding much less than expected and conversely subordinates initiated feeding significantly ( $p < 0.05$ ) more

Table III. Proportion of Time Dominants and Subordinates Initiated Entrance to the Experimental Area and Initiated Feeding Under Familiar and Unfamiliar Conditions When Tested in Groups. Proportions add to Over 100 Because More Than One Pup Could Act as an Initiator.

Group		Entrance		Feeding	
		Familiar	Unfamiliar	Familiar	Unfamiliar
A	Dom.	0.60	0.50	0.80	0.00
	Sub.	0.80	1.00	1.00	1.00
B	Dom.	0.60	0.50	0.60	0.00
	Sub.	1.00	0.75	1.00	1.00
C	Dom.	1.00	0.50	1.00	0.00
	Sub.	0.40	0.50	0.20	1.00
D	Dom.	0.00	0.00	0.60	0.25
	Sub.	1.00	1.00	0.80	1.00
total					
	Dom.	0.55	0.38	0.75*	0.06*
	Sub.	0.80	0.81	0.75	1.00*

\* significantly different than would be expected by chance ( $p < 0.05$ ).

than expected by chance when exposed to the novel stimulus. Thus, the results are consistent with the hypothesis that dominant animals are more hesitant in approaching food in the presence of novelty. There was no trend, however, in which subordinate pup initiated feeding when a novel stimulus was present.

#### Testing Coyotes Individually

Qualitative Results. As with the group experiments, during familiar conditions, the pups moved immediately to the feeding dish upon release from the den box. In contrast, when they encountered the novel object, the pups circled the feeding dish and novel object slowly, approaching and retreating frequently. Several pups did not eat before the session ended. When they did eat, they again showed approach-avoidance behavior, stretching out such that they kept as much of the body away from the dish as possible, and often moving back and forth away from the dish.

Quantitative Results. Only groups A and C showed significant differences in the amount of time required to resume feeding after the introduction of a novel stimulus (Table IV). In groups B and C, the subordinate individual which most often initiated feeding in unfamiliar conditions when in the group seemed to be habituating to the novel stimulus faster than the others of its group. In groups A



Table IV. Amount of Time it Took Pups to Commence Feeding With and Without a Novel Stimulus When Tested Alone Compared with the Number of Times the Pup Initiated Feeding When with the Group in the Presence of a Novel Stimulus.

Group	Pup	Mean Response Time (s)		No. Initiations when in group
		With Novelty	Without Novelty	
A	1	4.75	62.50	0
	2*	7.25	478.75	1
	3	9.00	38.25	2
	4*	10.25	780.50	1
B	1	4.00	359.00	0
	2	4.00	11.75	4
	3	5.00	90.75	0
C	1	23.00	514.80	0
	2*	320.25	1199.80	0
	3	19.00	212.30	4
D	1	16.00	81.25	1
	2	14.00	488.25	2
	3	13.25	71.00	3

\*The mean difference between sessions with and without the novel stimulus is significantly ( $p < 0.05$ ) different from the differences of the other pups from the group.

and D, however, dominant animals seemed to be habituating as fast to the novel stimulus as the subordinates. In all groups the amount of time it took the pups to initiate feeding in unfamiliar conditions when alone was longer than when they were in unfamiliar conditions with the group.

## DISCUSSION

The most dramatic differences in behavioral patterns between animals of different social ranks can be expected, I believe, in well established groups which exploit limited resources. This includes species with obligate grouping behavior such as the African wild dog (Lycaon pictus) (Frame et al. 1979) and species such as black-capped chickadees (Parus atricapillus) which live in small groups with stable membership (Smith 1976). Differences in responses should be greatest when resources can be controlled to the exclusion of others.

Coyote litters fulfill some of these conditions. Each litter is a small group of animals with a stable membership and with access to resources which can be controlled by the dominant animals. Coyotes have flexible social systems, however, and might not be as likely as species with more rigid social systems to show rank differences in behavioral responses. But in compensation, coyotes are opportunistic and may learn alternative methods of acquiring resources. Subordinate coyotes are therefore likely to adapt different strategies of resource acquisition. In spite of the coyotes' flexible social structure, the groups in this study exhibited consistent social rank differences in response to novel objects in a familiar environment. This phenomenon may therefore be found in other species, especially those which more

often live in stable groups.

Novel stimuli can be associated with danger and increased mortality (e.g. Barnett 1963; Hibler 1977). An animal will learn which conditions are dangerous through experience and stimulus generalization, and will habituate to stimuli not paired with aversive stimulus. Although the novel objects in this study were never specifically associated with increased danger, they represented a similar situation.

There are at least three hypotheses that may help to explain why, when within the group, subordinates are less conservative than higher-ranking animals in unfamiliar and potentially dangerous situations. First, because dominants control access to resources, lower-ranking animals may be more hungry (see Murton et al. 1966) and thus more apt to take risks than higher-ranking animals (Hegner in press). Second, the dominants may also be holding back, while lower-ranking animals determine the risks involved in exploring new conditions or exploiting new resources (Rohwer & Ewald 1981; Katzir 1982, 1983). Once the level of risk has been determined, dominants can assert control over the resources. Finally, I believe, dominant animals may in some cases display caution to avoid attracting attention by being alone spatially or behaviorally. In many groups, deviation from the activity of the group is dangerous due to a decrease in the effectiveness of the "dilution effect" (Krebs & Davies

1981).

Only one of these hypotheses is very helpful at explaining the results of this study. First, since the coyotes in this study were fed equally, presumably motivational differences due to different hunger levels were not a factor. Second the "increased danger" due to a loss in the protection offered by the dilution effect should not be an important factor with carnivores which do not necessarily live in large groups. So the behavioral differences of the coyotes can best be explained by the danger inherent in unfamiliar circumstances and the differential ability of the individuals of different social rank to acquire resources. The control of resources by dominant animals appears to force the subordinates to be less conservative in acquiring resources.

This control of resources by dominants can force subordinates to be less conservative either only around higher-ranking animals, or under a wide variety of conditions. The results of the individual tests to determine if the individuals behaved differently when away from the others in the group were inconsistent. When by themselves several of the pups responded to the novel stimuli the same as they did when they were in the group. Others, however, did not maintain the same response patterns. One can therefore only suspect that the phenomenon can not be explained solely by the two alternatives and the presence of the other group members may be an important influence.

Although not demonstrated in each of the groups in this study, it is likely that animals of different social ranks will develop patterns of responses in the group which they will retain later. By having to work harder to obtain resources, subordinates may develop more versatile responses to future problems. So even if subordinates revert to more conservative responses in some situations when alone, they may continue to be less cautious in other circumstances. For example they may be better at methods of resource acquisition requiring versatility. Supporting this contention are a variety of studies with rats (Rattus norvegicus) (Constanzo et al. 1975), crayfish (Cambarus virillus) (Constanzo et al. 1972) and crab-eating macaques (M. fascicularis) (Bunnel 1980; Bunnel et al. 1980), which demonstrate that subordinates learn new behavioral responses faster than dominants.

There are several aspects of the experimental design which could have contributed to the lack of trends in the individual tests. First, the timing of group formation may be an important factor in determining if dominant-subordinate interactions will influence the behaviors of the pups when alone. The pups which did not maintain the same response patterns to novel stimulus when alone and when with the group were from the two groups which were combined late (at 7 and 8 weeks of age). There might therefore be a critical period which will affect the extent dominance interactions will influence individual

behaviors. Second, it was impossible to exert total environmental control, so the conditions differed slightly for each pup. Similarly, it was impossible to control individual experiences. Pups also may have different abilities to generalize from one novel stimulus to another. Although there were definite individual differences, the phenomenon of rank differences in responses of the pups in a group to unfamiliar conditions was very clear.

The distinct behaviors of animals of different social rank has important implications for research. Many techniques used to study animals involve the introduction of novel stimuli. Things such as traps and scent stations may only attract a segment of the population, biasing the results (Balph & Balph 1981; Harris 1983). If subordinate animals are more responsive to novel objects, they may have higher capture probabilities than dominant animals. The results of this study suggest, however, that such differences in responsiveness will be most important when the animals are in a group, and will be less important when animals are alone.

Behavioral differences may also have implications on dispersal. Coyotes have been found in a wide variety of habitats, including major urban areas (Gill 1970) and are presently rapidly expanding their range (Bekoff 1977; Vaughan 1983). Understanding individual behavioral differences may help determine which animals are more likely to successfully disperse into these areas. In a totally new

environment, dominants and subordinates may respond similarly to novel stimuli. Studies with coyotes suggest that they tend to avoid novel objects when in familiar environments, but will approach them in unfamiliar areas (Hibler 1977; Harris 1983; see also Calhoun 1963). Dispersing coyotes, therefore, are more prone to capture or mortality. But subordinates which have developed more versatile behaviors may be smarter due to past experience. If dominants and subordinates have similar chances of avoiding the dangers of dispersal, more adaptable individuals should be more successful.

The behaviors of dispersing animals may also depend in part on whether they disperse individually or in groups. Coyote pups disperse either singly or leave their parents but remain with littermates until a later time (Camenzind 1978). A dispersing dominant may benefit from the presence of lower-ranking animals if subordinates aid in determining potential danger and discover adaptable means of obtaining important resources.

Many of the factors influencing the behavioral differences of dispersing animals may also be important in determining which animals will adapt to changing environments or which are more likely to learn new predatory methods. Subordinate animals, if they are less conservative, may be more likely to start killing livestock, for example.



When in groups, coyotes clearly demonstrate distinct rank differences in response to novel stimuli. Although not shown in this study, there is reason to believe that animals will retain some behavioral patterns they learn while in the groups, and employ them at other times. The behaviors and conditions most strongly influenced by past dominant-subordinate interactions still require investigation.

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